CHAPTER 2
RESILIENCE AND ADAPTIVE CYCLES

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Make things as simple as possible, but no simpler.
—Albert Einstein

The purpose of this chapter, and the succeeding one, is to deepen understanding of the fifth of the worldviews described in Chapter 1—that of Nature Evolving. It is another step in the effort to develop theories for sustainable futures.

What follows in this chapter is an initial comparison of the structure and dynamics of ecological and social systems from the perspective of ecosystem ecologists. We draw on ecological examples and theory and on lessons from examples of regional ecosystem management in order to develop new concepts to explain the organization and dynamics of complex adaptive systems. We only hint at similarities in social and economic systems—just enough that, in later chapters, they can be the source for discovering the limits of the theory.

We begin by abstracting key elements of our understanding regarding how ecosystems are organized and operate. We then use examples of different ecosystems to develop several variants of a heuristic model of change that involves four phases: exploitation, conservation, creative destruction, and renewal, which constitute an adaptive cycle. We end with questions emerging from puzzles and paradoxes not well treated by the model presented, especially in terms of cross-scale dynamics.

Key Features of Ecosystems

The accumulated body of empirical evidence concerning natural, disturbed, and managed ecosystems identifies key features of ecosystem structure and function that can be distilled into the following points:

- Change is neither continuous and gradual nor consistently chaotic. Rather it is episodic, with periods of slow accumulation of natural capital such as biomass, physical structures, and nutrients, punctuated by sudden releases and reorganization of those biotic legacies (Franklin and MacMahon 2000) as the result of internal or external natural disturbances or human-imposed catastrophes. Rare events, such as hurricanes or the arrival of invading species, can unpredictably shape structure at critical times or at locations of increased vulnerability. The results of these rare events represent "frozen accidents" whose influence can shape the future for long periods. Irreversible or slowly reversible states can exist; once the system flips into such a state, only explicit management intervention can return its previous self-sustaining state, and even then recovery is not assured (D. Ludwig et al. 1997).

  Critical processes function at radically different rates that span several orders of magnitude, but these rates cluster around a few dominant frequencies. Episodic behavior is caused by interactions between fast and slow variables.

- Spatial attributes are neither uniform nor scale invariant over all scales. Rather, productivity and textures are patchy and discontinuous at all scales, from the leaf to the landscape to the planet. There are several different ranges of scales, each with different attributes of architectural patchiness and texture and each controlled by a specific set of abiotic and biotic processes. They make attributes of the natural world lumpy, rather than continuous (Holling 1992), thereby concentrating resources and opportunities at particular scales.

  Therefore, scaling up from small to large cannot be a process of simple aggregation: nonlinear processes organize the shift from one range of scales to another.

- Ecosystems do not have a single equilibrium with homeostatic controls to remain near it. Rather, multiple equilibria commonly define functionally different states. Normal movements of variables between states maintain structure, diversity, and resilience. Nonlinear features of processes of predation, reproduction, competition, and nutrient dynamics create the multiple equilibria. Stochastic forces and interactions between fast variables and slow ones mediate the movements of variables among those equilibria (Carpenter 2000).

  On the one hand, destabilizing forces are important in maintaining diversity, resilience, and opportunity. On the other hand, stabilizing forces are important in maintaining productivity and biogeochemical cycles.

- Policies and management that apply fixed rules for achieving constant yields (e.g., fixed carrying capacity of cattle or wildlife, or fixed sustainable yield of fish or wood), independent of scale, lead to systems that increasingly lose resilience—i.e., to systems that suddenly break down in the face of disturbances that previously could be absorbed (Holling 1986, 1995).

  Ecosystems are moving targets, with multiple futures that are uncertain and unpredictable. Therefore, management has to be flexible, adaptive, and experimental at scales compatible with the scales of critical ecosystem functions (Walters 1986; Gunderson et al. 1995b).

Those key features provide the minimal set of strategic criteria that need to be satisfied by any theory of adaptive change appropriate for ecosystems. They lead to a view of ecosystems that can make sense only if it is compatible with some version of both Nature Resilient and Nature Evolving. We propose, moreover, that the same criteria, with several additions unique to human systems, are equally necessary for models of human institutions, organizations, and society. To set the stage we need to define what we mean by stability, variability, and resilience of a system.

Two Ways of Looking at Stability

Resilience has been defined in two very different ways in the ecological literature. These differences in definition reflect which of two different aspects of stability is emphasized. The consequences of those different aspects for ecological systems were first emphasized by Holling (1973b) in order to draw attention to the tension created between efficiency on the one hand and persistence on the other, or between constancy and change, or between predictability and unpredictability. One definition focuses on efficiency, control, constancy, and predictability—all attributes at the core of desires for fail-safe design and optimal performance. Those desires are appropriate for systems where uncertainty is low, but they can be counterproductive for dynamic, evolving systems where variability and novelty result in high uncertainty. The other definition focuses on persistence, adaptiveness, variability, and unpredictability—all attributes embraced and celebrated by those with an evolutionary or developmental perspective. The latter attributes are at the heart of understanding and designing for sustainability.

The first definition, and the more traditional, concentrates on stability near an equilibrium steady state, where resistance to disturbance and speed of return to the equilibrium are used to measure the property (Pimm 1984; Tilman and Downing 1994). We term this *engineering resilience* (Holling 1995; Holling and Meffe 1996).

The second definition emphasizes conditions far from any equilibrium steady state, where instabilities can flip a system into another regime of behavior—i.e., to another stability domain (Holling 1973b). In this case

resilience is measured by the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior. This we term *ecosystem resilience*.

These studies and examples increasingly suggest that effective and sustainable development of technology, resources, and ecosystems requires ways to deal not only with near-equilibrium efficiency but also with the reality of more than one equilibrium.

These two aspects of a system's stability have very different consequences for evaluating, understanding, and managing complexity and change. We argue here that sustainable relationships between people and nature require an emphasis on the second definition of resilience, i.e., as the amount of disturbance that can be sustained before a change in system control and structure occurs—ecosystem resilience. That shifts the management and policy emphasis from micro, command-and-control approaches to ones that set overall conditions to allow adaptive enterprises (Holling and Meffe 1996). That interplay between stabilizing and destabilizing properties is at the heart of present issues of development and the environment—global change, biodiversity loss, ecosystem restoration, and sustainable development.

Exclusive emphasis on the first definition of resilience, engineering resilience, reinforces the dangerous myth that the variability of natural systems can be effectively controlled, that the consequences are predictable, and that sustained maximum production is an attainable and sustainable goal. Gunderson, Holling, and Light (1995a) present examples showing why that leads to the pathology of resource management (Chapter 1). The very success of limiting variability of a target leads to the unperceived shrinkage of stability domains. As ecosystem resilience is lost, the system becomes more vulnerable to external shocks that previously could be absorbed.

These are two contrasting aspects of stability. One focuses on maintaining *efficiency* of function (engineering resilience); the other focuses on maintaining *existence* of function (ecosystem resilience). Those contrasts are so fundamental that they can become alternative paradigms whose devotees reflect traditions of a discipline or of an attitude more than of a reality of nature.

Those who emphasize the near-equilibrium definition of engineering resilience, for example, draw predominantly from traditions of deductive mathematical theory (Pimm 1984) where simplified, untouched ecological systems are imagined. Another example arises from experimental manipulation of organisms where the scale is limited to small enclosures or field quadrats (Tilman and Downing 1994). Yet another example is from traditions of engineering, where the motive is to design systems with a single operating objective (Waide and Webster 1976; De Angelis et al. 1980). Such partial representations make the mathematics more tractable, the experiments more controllable, and the designs more functionally optimal. There is an implicit assumption of global stability—i.e., there is only one equilibrium steady state, or, if other operating states exist, they can be avoided with appropriate safe-

guards, so that the variables are maintained near the "best" equilibrium, well away from a dangerous break point. There are also the assumptions that it is sufficient to represent or manipulate only fast, local variables and that slowly changing, extensive variables and their interactions can be ignored.

Those who emphasize the stability domain definition of resilience (i.e., ecosystem resilience), on the other hand, come from traditions of applied mathematics and applied resource ecology at the scale of ecosystems and of landscapes. Examples are the dynamics and management of freshwater systems (Fiering 1982); of forests (Holling et al. 1976a); of fisheries (Walters 1986); of semiarid grasslands (Walker 1981); of lakes (Scheffer 1998; Carpenter, Ludwig, and Brock 1999; Janssen and Carpenter 1999); and of interacting populations in nature (Sinclair et al. 1990; Dublin et al. 1990). Because these studies are rooted in inductive rather than deductive theory formation and in experience with the impacts of management disturbances at multiple scales, the reality of flips from one operating state to another cannot be avoided. Clear lakes can turn into turbid, anoxic pools, grasslands into shrub-deserts, and forests into grasslands. D. Ludwig et al. (1997) provide a fine exploration of the mathematical underpinnings to these different views of resilience with examples from natural and managed systems. Scheffer (1999) provides a lucid and accessible example of multistable behavior in European lakes and the management strategies for dealing with them.

In ecology, the causes and conditions of multiple equilibria were challenged by Sousa and Connell (1985), who analyzed time series data of animal populations. This is an example of a laudably skeptical effort to invalidate a novel proposition. It came to an erroneous conclusion because the data systems used to test the proposition were defined too simply. They did not have the level of requisite complexity needed. They lacked the minimally essential features for answering the question. The example is instructive for other issues: of, for example, the detection and use of pattern in analyzing any long time series—ecological, paleoecological, climatic, or financial—or of spatial or geometric patterns. Causation was ignored and the relevant duration of data was defined by the assumption that fast variables alone defined multistable properties.

For example, Sousa and Connell (1985) presumed that 40 years of available data covering forty generations of the forest insect, the spruce budworm, was sufficient to test for multistable states in the budworm/forest system. It certainly seems long enough to data-starved ecologists! However, slow variables, like the foliage accumulation of the maturing forest, set by a generation time of 80–120 years for the trees, slowly change the stability conditions for fast ones (Box 2-1). The minimal need is for a time series that covers three generations of the trees (at least 300 years). It is no wonder that moving multiple lines of evidence, understanding of causation, and recognition of requisite levels of simplicity has been the only way to establish the reality and importance of multistable states. That is what Carpenter (2000) has summarized in a masterful review of the empirical evidence. It has taken

twenty-five years to establish that multistable states are, in fact, common in ecosystems, common enough that management dare not ignore them, because of the potential high cost of doing so.

Box 2-1. Spruce-Fir Forests and Insect Outbreaks

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One classic example of the adaptive cycle shown in Figure 2-1 is the dynamics of the spruce-fir forest of eastern North America. The patterns produced depend on the nonlinear processes that trigger and organize the release and reorganization phase. One of the primary triggers for release in the eastern balsam fir forest of North America is an insect outbreak species, the spruce budworm. Two principal stability states exist. One is with low budworm populations and young, growing trees. The other is with high budworm populations and mature trees. The latter condition is associated with so much defoliation that the trees die over extensive areas. Prior to harvesting and management, up to 80 percent of the balsam fir trees in central eastern Canada and the United States would die from budworm attacks at intervals of from 40 to 130 years. It is an entirely natural phenomenon, part of forest renewal, and is an example of alternating stable states.

The release phase occurs because the maturing forest accumulates a volume of foliage that eventually dilutes the effectiveness of the search by insectivorous birds for budworm. So long as predation by birds is high, as it is in younger stands, it is sufficient, with other mortality agents, to control budworm populations at low densities. Essentially, a lower equilibrium density for budworm is set by a "predator pit" (Clark et al. 1979; Holling 1988) in a stability landscape during the phase of slow regrowth of the forest. This stability pit eventually collapses as the trees mature, to release an insect outbreak and reveal the existence of a higher equilibrium. A more formal mathematical representation is given in Ludwig et al. (1978). A similar argument can be described for release by fire, as a consequence of the slow accumulation of fuel as a forest ages.

To summarize and generalize this example: For long periods in a regrowing forest, the slow variable (trees) controls the faster (budworm or fire) and intermediate-speed variables (foliage or fuel) until a stability domain shrinks to the point where the fast variables for a brief time can assume control of behavior and trigger a release of the accumulated capital.

Back to Myths of Nature

The features summarized in the two preceding sections suggest that the images of Nature Flat and Nature Anarchic described in Chapter 1 are wrong in their incompleteness. Both myths are wrong, because there are clearly regulatory forces that cause ecosystems to pause for longer or shorter periods in one set of relationships and one assemblage of species in one place. Some call those ecosystems. But Nature Balanced is equally wrong. There are strong destabilizing forces that introduce variability, sometimes abrupt, and that variability is the source of much of the diversity of species and the richness of nature we see. Nature Resilient would seem to provide an amalgam of both. It does that, but is it satisfactory? Is it sufficient?

Consider the consequences if a system were highly resilient. Is that entirely a desired condition? Such a system would not change in any fundamental way. In the face of large disturbances, variables would shift and move, but the system would maintain its controls and structure. If that is common, how do we explain the dramatic, changing character of landscapes over geological time? The answer might simply be that the resilience is never infinite and is eventually swamped by some external, large-scale change, and the system is replaced by something else. For example, some ten thousand years ago (very recent in geologic time frames) the treasured Everglades of southern Florida were not wetlands, but a dry savanna. Had we been living then, would we, as people concerned with the conservation of nature, have sought to maintain that savanna state as desirably pristine, holding back the rising seas as glaciers melted? Placing fingers in the dikes we built? Denying the reality of climate change? Is it desirable to have a goal of preserving and protecting systems in a pristine, static state?

These tough questions are not normally addressed by conservationists or environmentalists. They are tough also because they challenge the authors' own values and desire to sustain a rich and diverse natural world. But in a complex evolving world, the function and future of linked human and natural systems evolve and are highly uncertain. Efforts to freeze or restore to a static, pristine state, or to establish a fixed condition are inadequate, irrespective of whether the motive is to conserve nature, to exploit a resource for economic gain, to sustain recreation, or to facilitate development. Short-term successes of narrow efforts to preserve and hold constant can establish a chain of ever more costly surprises—versions of the pathology of resource management and development described in Chapter 1.

It helps to switch, for a moment, from thinking of ecosystems to thinking of sociopolitical ones. Clearly, locking a sociopolitical system into a fixed set of controls can transparently create an unsustainable political system. For a time, at least, the Soviet Union was an immensely resilient "dictatorship of the bureaucracy" (Levin, Barrett et al. 1998). Its very resilience preserved a maladaptive system. What this suggests for social systems, as well as ecological ones, is that resilience is not an ideal in itself. Moreover, it is not a fixed

quantity that defines a system, but a dynamically varying one. Resilience can be the enemy of adaptive change. That is, the myth of Nature Resilient is too partial and static in a structural sense.

But what do we do? What is enduring and must always be so? What is sustainable? We need a transition from the structurally static view of Nature Resilient to a structurally dynamic view of Nature Evolving.

Conserving the elements we have is not the goal for a search for what is enduring. Otherwise, we would still be blacksmiths and buggy-whip makers. The challenge, rather, is to conserve the ability to adapt to change, to be able to respond in a flexible way to uncertainty and surprises. And even to create the kind of surprises that open opportunity. It is this capacity that a view of an evolving nature should be all about—i.e., maintaining options in order to buffer disturbance and to create novelty. A living system cannot be kept within some desirable state or on some desirable trajectory if adaptive capacity is continuously lost.

The purpose of theories such as panarchy is not to explain what is; it is to give sense to what might be. We cannot predict the specifics of future possibilities, but we might be able to define the conditions that limit or expand those future possibilities. As a consequence, the properties we need to choose are not those chosen to describe the existing state of a system and its behaviors, but rather ones chosen to identify the properties and processes that shape the future. This introductory exploration identifies three requirements in our quest for a theory of adaptive change:

- First, the system must be productive, must acquire resources and accumulate them, not for the present, but for the potential they offer for the future.

- Second, there must also be some sort of shifting balance between stabilizing and destabilizing forces reflecting the degree and intensity of internal controls and the degree of influence of external variability.

- Third, somehow the resilience of the system must be a dynamic and changing quantity that generates and sustains both options and novelty, providing a shifting balance between vulnerability and persistence.

The Adaptive Cycle

In case examples of regional development and ecosystem management (Gunderson et al. 1995b), three properties seemed to shape the future responses of the ecosystems, agencies, and people:

- the potential available for change, since that determined the range of options possible;

- the degree of connectedness between internal controlling variables and processes, a measure that reflects the degree of flexibility or rigidity of such controls—i.e., their sensitivity or not to external variation;
- the resilience of the systems, a measure of their vulnerability to unexpected or unpredictable shocks.

Note, at this stage, we choose very general properties because our initial goal is to develop a framework of adaptive change that has generality. Such a framework is hardly a theory, therefore. Rather, it is a metaphor to help interpret events and their gross causes.

The original concept of the adaptive cycle and the review described in this section emerged from experience with productive ecosystems that exist in temperate regions of the world—places where rainfall is consistent, although seasonally variable. They specifically included the boreal coniferous forests of the Northern Hemisphere, productive grasslands on deep soils, and temperate deciduous forests. But many ecosystems have developed in very different conditions—coral reefs, nutrient-poor savannas with low and episodic rainfall, open-ocean pelagic communities, shallow and deep lakes, nutrient-poor tropical forests. In the remainder of this chapter we review the cycle as it was described for productive temperate ecosystems and possible similarities in human organizations and economies. To test its limits, we then consider more extreme types of ecosystems, hoping to discover where the metaphor breaks down. To push that exploration of limits further, we also start to explore large human organizations—bureaucratic and industrial organizations. In the next sections, we review properties of the original adaptive cycle metaphor, beginning with two of the key properties, potential and connectedness, before adding the third property, resilience.

Two Dimensions of Change: Potential and Connectedness

The traditional view of ecosystem succession has been usefully seen as being controlled by two functions: *exploitation*, in which rapid colonization of recently disturbed areas is emphasized; and *conservation*, in which slow accumulation and storage of energy and material are emphasized. In ecology the species in the exploitive phase have been characterized as r-strategists and in the conservation phase as K-strategists. These are names drawn from the traditional designation of parameters of the logistic equation (r represents the instantaneous rate of growth of a population, and K the sustained plateau or maximum population that is attained; Pearl 1927). The r-types are characterized by extensive dispersal ability and rapid growth in an arena where scramble competition succeeds (the first to get the prize wins), while the K-strategists tend to have slower growth rates and flourish in an arena of contest competition (resources become divided and sequestered to separate

uses). To an economist or organization theorist, those functions could be seen as equivalent to the entrepreneurial market for the exploitation phase and the bureaucratic hierarchy for the conservation phase. Baron, Burton, and Hannan (1998) provide a very detailed study of the forces that determine different patterns such as path dependence in the evolution of bureaucracy, even when firms face intense competition.

But subsequent ecological understanding indicates that two additional functions are needed, as summarized in Figure 2-1. The first revision is that of *release*, or "creative destruction," a term borrowed from the economist Schumpeter (1950, and as reviewed in Elliott 1980). The tightly bound accumulation of biomass and nutrients becomes increasingly fragile (overconnected, in systems terms) until suddenly released by agents such as forest fires, drought, insect pests, or intense pulses of grazing. We designate that as the omega (Ω) phase.

The second additional function is one of *reorganization*, in which soil processes minimize nutrient loss and reorganize nutrients so that they

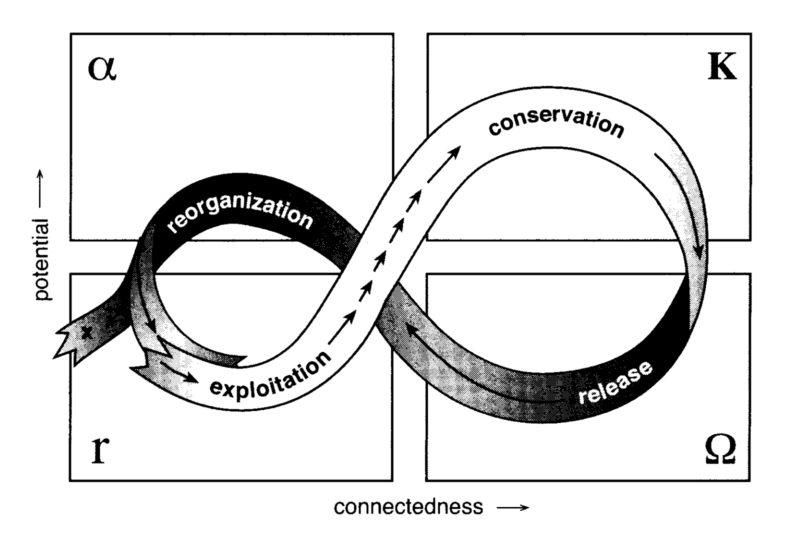


Figure 2-1. A stylized representation of the four ecosystem functions (r, K, Ω, α) and the flow of events among them. The arrows show the speed of that flow in the cycle, where short, closely spaced arrows indicate a slowly changing situation and long arrows indicate a rapidly changing situation. The cycle reflects changes in two properties: (1) Y axis—the potential that is inherent in the accumulated resources of biomass and nutrients; (2) X axis—the degree of connectedness among controlling variables. Low connectedness is associated with diffuse elements loosely connected to each other whose behavior is dominated by outward relations and affected by outside variability. High connectedness is associated with aggregated elements whose behavior is dominated by inward relations among elements of the aggregates, relations that control or mediate the influence of external variability. The exit from the cycle indicated at the left of the figure suggests, in a stylized way, the stage where the potential can leak away and where a flip into a less productive and organized system is most likely.

become available for the next phase of exploitation. Part of this reorganization involves the transient appearance or expansion of organisms that begin to capture opportunity—the pioneer species. Their source is from growth of previously suppressed vegetation, from germinating seeds stored in seed banks accumulated from the past, and from dispersal of both endemic and exotic propagules from distant places. The reorganization phase is essentially equivalent to one of innovation and restructuring in an industry or in a society—the kinds of economic processes and policies that come to practical attention at times of economic recession or social transformation. We designate that as the alpha (α) phase.

If the omega phase represents the end, then it is immediately followed by the alpha phase, the beginning—a progression at least as interesting philosophically as it is ecologically.

During this cycle, biological time flows unevenly. The progression in the ecosystem cycle proceeds from the exploitation phase (r phase, Figure 2-1) slowly to conservation (K phase), very rapidly to release (Ω phase), rapidly to reorganization (α phase), and rapidly back to exploitation. During the slow sequence from exploitation to conservation, connectedness and stability increase and a "capital" of nutrients and biomass is slowly accumulated and sequestered. Competitive processes lead to a few species becoming dominant, with diversity retained in residual pockets preserved in a patchy landscape. While the accumulated capital is sequestered for the growing, maturing ecosystem, it also represents a gradual increase in the potential for other kinds of ecosystems and futures. For an economic or social system, the accumulating potential could as well be from the skills, networks of human relationships, and mutual trust that are incrementally developed and tested during the progression from r to K. Those also represent a potential developed and used in one setting that could be available in transformed ones.

As the progression to the K phase proceeds, the accumulating nutrient and biomass resources become more and more tightly bound within existing vegetation, preventing other competitors from utilizing them. The potential for other use is high, but it is expropriated and controlled by the biota and processes of the ecosystem in place. That is, the system's connectedness increases, eventually to become overconnected and increasingly rigid in its control. The actual change is triggered by agents of disturbance such as wind, fire, disease, insect outbreak, and drought or a combination of these. The resources sequestered in vegetation and soil are then suddenly released and the tight organization is lost. Its potential for other uses drops until the released resources that remain are reorganized so that the potential for other uses reemerges in the α phase.

A number of such patterns have been discovered in several terrestrial and near terrestrial ecosystems at landscape scales (Boxes 2-2 and 2-3). In all instances, periodic flips from one stable state to another are mediated by changes in slow variables that suddenly trigger a fast-variable response, or escape.

Box 2-2. Alternative Stable States

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Alternative stable states have been described for a diverse variety of terrestrial and near terrestrial ecosystems. In each of these cases, periodic flips from one state to another are mediated by changes in slow processes that suddenly trigger a fast-process response, or escape from a state. The following cases provide examples:

Meta-population dynamics. A connected set of populations can exist at either a high-density connected state or a low-density fragmented state. In a landscape composed of potential habitats, the population of a particular habitat depends on its neighboring sites. If the population at a site becomes extinct, the probability of recolonization increases with the aggregate size of the surrounding populations. This effect produces a positive feedback between the density of a region's population and the likelihood that that region's population can maintain itself. Consequently, a regional population can rapidly decline if its population begins to fail to recolonize potential sites, because this further reduces the probability of recolonizing sites (Hanski et al. 1995).

Shallow lakes. In shallow lakes the interactions among turbidity, nutrients loading, vegetation, and fish produce two alternative stable states (Scheffer et al. 1993). Lakes can exist either in a state in which water is clear and dominated by rooted aquatic vegetation, or in a state in which water is turbid and dominated by phytoplankton. The large, rooted plants stabilize the substrate sediment, reduce turbidity, encourage the stabilization of nutrients, and provide refugia for phytoplankton-consuming fish. If rooted plants are eliminated, the resulting turbidity blocks light for plants, and resuspended sediment makes nutrients available to phytoplankton. Lakes usually switch between states due to a combination of changes. For example, a clear lake can lose rooted plants and become turbid due to an increase in nutrient loading, a decrease in algae-eating fish, an inflow of sediment, or the removal of vegetation (Blindow et al. 1993). Similarly, a turbid lake can be made clear by reducing the population of bottom-foraging, turbidity-increasing fish, or by decreasing the number of fish that eat algae eating fish.

Reefs. Corals, surface algae, and macro-algae are all components of coral reef communities. Changes in the extent of predation on algae by fish and sea urchins, changes in nutrient concentrations, and the presence of new areas to grow control

switches between states (Knowlton 1992). Consequently, shifts between stable states can be influenced by disturbance events that provide new areas for recruitment, resuspend sediments, and cause variations in the population of algae eaters (Hughes 1994). Fishing and variation in recruitment can strongly influence fish populations, while the interaction of density-dependent recruitment and circulation patterns allows sea urchins to exist at self-maintaining high- or low-density states (McClanahan et al. 1996). These interactions suggest that reefs can exist in three self-maintaining states: coral-fish, turf algae-urchins, and macro-algae (Done 1992; Knowlton 1992).

Sea otters, sea urchins, and kelp forests. Along the coast of the northern Pacific, rocky near-shore communities can be dominated by either dense stands of kelp or few kelp and large concentrations of sea urchins. The presence of these states is controlled by the presence of sea otters that prey upon sea urchins. In the absence of sea otters, urchin populations can increase to a density that prevents kelp forests from establishing. On the other hand, when sea otters are present, their predation on sea urchins allows key kelp forests to become established (Estes and Duggins 1995).

Fire in North Florida. Oak trees and pine trees dominate sandhill communities in northern Florida. Fire mediates the competitive relationships between the abundance of these two species. Longleaf pine (*Pinus palustris*) is a particularly fire-tolerant pine species. Mature longleaf pines shed needles that provide good fuel for ground fires, and young longleaf pines can survive ground fires. Young hardwoods are intolerant of fire, and mature hardwoods shed leaves that suppress the buildup of fuel for ground fires. This lack of fuel tends to suppress fire in hardwood stands, encouraging the growth of more hardwoods, while fuel accumulation in stands of pine tends to encourage fire, suppressing hardwoods and encouraging the growth of pine (Glitzenstein et al. 1995; Rebertus et al. 1989).

Fire spreads itself from burning sites into combustible sites. A fire that is surrounded by noncombustible sites will be unable to spread and will extinguish itself. The mutual reinforcement between fire and longleaf pine will occur only if the fires are started frequently and are able to spread across a large area. Otherwise, sites will burn infrequently, and fire-susceptible vegetation will be replaced by fire-suppressing vegetation. The ability of fire to spread, and consequently the rate at which patches of hardwood or pine either grow or shrink, is determined by the distribution of hardwoods and pine across the landscape. The relative proportion of

continues

hardwood and pine in the area surrounding a site will determine the succession of a forest site.

Elephants, fire, and savanna. Dublin et al. (1990) propose that the elephants and fire interact with competition between grasses and trees to produce two alternative stable states in the Serengeti-Mara. Fire shifts from a woodland to a grassland state. Grassland is maintained by herbivores, particularly elephants, consuming young seedlings. However, this consumption is not sufficient to shift woodland to grassland, as it is significant only at low-seedling densities. Low-herbivore density and infrequent fire allow woodland regeneration to occur (Dobson 1995; Dublin 1995). For example, when rinderpest eliminated a large number of grazers, woodlands experienced a pulse of regeneration (Prins and Jeud 1993).

As the system shifts from α to r, some of the potential leaks away because of the collapse of organization; some of the accumulated resources literally leave the system. In addition, new entrants, those that survived to the α phase, and the "biotic legacies" of past cycles (Franklin and MacMahon 2000) begin to sequester and organize resources in a process that leads to the r species establishing "founding rights" over the remaining capital. The result of both processes lowers the potential from α to r.

Note that in a sustainable ecosystem, the accumulated resources that determine ecological potential might be eroded, might partially leak away, but are only partially reduced. If they were completely or largely eliminated, recovery would be impossible, and the system would slip into a different, degraded state. Such a condition would occur, for example, if species critical in maintaining structure and function became extinct. That has certainly happened in geological history with extinctions of large herbivores in North America at the end of the Pleistocene some ten thousand years ago. It has also occurred in Australia with the consequence of loss of a stable state (Box 2-3).

But in most swings of the cycle, there is sufficient carryover from cycle to cycle to sustain an ecosystem's possible states. Typically, the actual aggregate resources accumulated would take a different path than the trajectory of potential shown in the figure, modestly fluctuating in amount through one cycle. Or, as in the case of wetlands, like the Everglades, those resources could continually accumulate, cycle by cycle, stored in the immobilized accumulation of peat. The basic cycle of vegetation in the Everglades from ponds to sawgrass to fire takes in the order of decades. However, the accretion of five meters of peat in the Everglades occurs over multiple cycles on the order of a five-thousand-year period (Gleason 1984). What does change dramatically during a cycle in all such systems is the potential. It alternates between high potential in the α and K phases, lower potential in the r phase, and still lower potential in the Ω phase.

Box 2-3. Loss of an Alternative State?

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Occasionally, due to the loss of an important system component, transition between multiple states results in the elimination of a former stable state. The extinction of species that perform a critical ecological function can cause such irreversible transitions. Pleistocene extinctions may provide an example of such a transition.

Sediment cores from Australia show that about 100,000 years ago pollen from fire-tolerant plants and mangroves increased while other species declined. These increases were likely due to the increases in burning that are also documented by an increase in charcoal in the sediment cores. Increases in fire frequency would have allowed fire-tolerant plants to spread, while at the same time leaving more bare soil to be eroded and deposited as coastal sediment and providing increased habitat for mangroves. Similar climatic conditions had existed previously without increases of fire, which suggests that the arrival of humans may have been responsible (Kershaw 1988).

Flannery (1994) proposes that it was overhunting of Australia's large marsupial herbivores that caused this change, rather than anthropogenic modification of fire regimes. During the time in which humanity is thought to have been in Australia, fifty large and medium-sized marsupial herbivores became extinct, along with several large herbivorous birds and turtles. If these herbivores lived similarly to existing large herbivores (Dublin et al. 1990; Owen-Smith 1989), then their extinction also likely eliminated their maintenance, through grazing, physical disturbance, and nutrient cycling, of a variety of vegetative patterns across the landscape. The removal of this small-scale patterning, and a buildup of fuel, may have facilitated the occurrence of larger and more intense fires. Such fires reduce local nutrient cycling by causing larger-scale erosion. Flannery suggests that this process caused the expansion of heathlands of fire-tolerant species at the expense of fire-intolerant vegetation adapted to herbivory. Without large herbivores to prevent and fragment vegetation, an ecosystem of fire and fire-dominated plants could expand at the expense of a system of large herbivores and herbivore-adapted plants. Flannery argues that hunting and use of fire removed large herbivores and volatilized accumulated nutrients, irreversibly switching the system from a more productive state, dependent on rapid nutrient cycling, to a less productive state, with slower nutrient cycling, maintained by fire.

Human enterprises can have similar behavior, as, for example, when corporations such as IBM and General Motors accumulate rigidities to the point of crisis, followed by efforts to restructure (Hurst and Zimmerman 1994; Hurst 1995). The key test of the limits of the metaphor is not whether resources and potential increase from r to K, but whether rigidities inevitably do so as well. Are there designs and actions that allow growth without increasing rigidities to the point of collapse? That kind of test is what is needed to adapt and expand the metaphor.

But before we can start comparing and contrasting different systems in order to discover where the scheme breaks down, it is necessary to add the resilience dimension to those of connectedness and potential. That addition disentangles some of the inconsistencies that emerge when the adaptive cycle is applied to specific situations. It is necessary to add vulnerability to change in addition to the other two properties of limits of change (potential) and degree of internal control over variability (connectedness). That property of vulnerability is determined by the resilience of the system.

Adding Another Dimension: Resilience

Figure 2-2 adds the third dimension, resilience. The appearance of a figure 8 in the path of the adaptive cycle (as in Figure 2-1) is shown to be the consequence of a projection of a three-dimensional object onto a two-dimensional plane. We can view that three-dimensional object from different perspectives, in order to emphasize one property or another. Figure 2-2 revolves the object to expose the resilience axis.

As the phases of the adaptive cycle proceed, a system's ecological resilience expands and contracts as suggested in Figure 2-2. Note that the myth of Nature Resilient described in Chapter 1, in contrast, sees resilience of a system as a fixed quantity for the whole system. In that view, a system is resilient or not in various fixed degrees. But here we see resilience expanding and contracting within a cycle as slow variables change. We had to recognize that feature as an essential attribute for the myth of Nature Evolving and for resolving paradoxes encountered in examining specific examples of sustainable change.

The essential requirement is to recognize that conditions are needed that occasionally foster novelty and experiment. Those become possible during periods when connectedness is low and resilience is high. The low connectedness permits novel reassortments of elements that previously were tightly connected to one another. The high resilience allows tests of those novel combinations because system-wide costs of failure are low. Those are the conditions needed for creative experimentation. This recognition of resilience varying within a cycle is the first element added that provides a way to reconcile the delicious paradoxes of conservative nature versus creative nature, of sustainability versus creative change. Other additions concerning the nature of hierarchies will be explored in the next chapter.

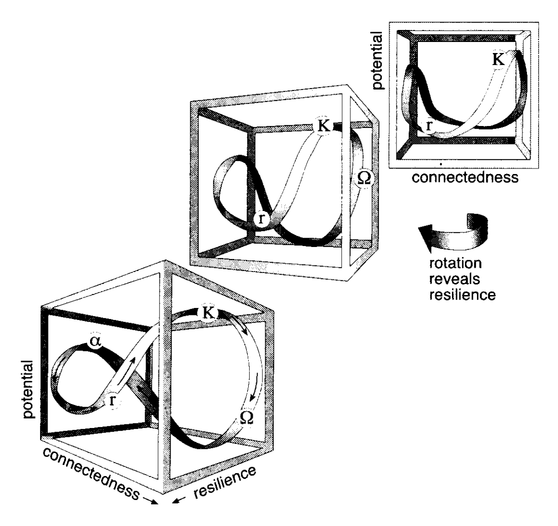


Figure 2-2. Resilience is another dimension of the adaptive cycle. A third dimension, resilience, is added to the two-dimensional box of Figure 2-1, showing that resilience expands and contracts throughout the cycle. Resilience shrinks as the cycle moves toward K, where the system becomes more brittle. It expands as the cycle shifts rapidly into a "back loop" to reorganize accumulated resources for a new initiation of the cycle. The appearance of a figure 8 in Figure 2-1 is shown to be the consequence of viewing a three-dimensional object on a two-dimensional plane.

The α phase begins a process of reorganization to provide the potential for subsequent growth, resource accumulation, and storage. At this stage, the ecological resilience is high, as is the potential. But connectedness is low, and internal regulation is weak. There is a wide stability region with weak regulation around equilibria, low connectivity among variables, and a substantial amount of potential available for future development. Because of those features, it is a welcoming environment for experiments, for the appearance and initial establishment of entities that otherwise would be out-competed. As in good experiments, many will fail, but in the process, the survivors will accumulate the fruits of change.

But the same condition of low connectedness results in the system becoming "leaky." This leaky-ness is a signal of the α phase. It was first demonstrated empirically by Bormann and Likens (1981) in the famous Hubbard Brook experiment. Various treatments (e.g., tree removal, herbicide) of a small, forested watershed in New England mimicked a K to Ω event. The water flow from the watershed was monitored and showed a pulse of nutrient loss that, within weeks, was slowed and stabilized as the ecosystem processes became reorganized. The same leaky phase has been described for semiarid savannas subject to the persistent disturbance of sheep grazing. If that continues, as it can when ranchers have no viable economic alternative, the rangelands progressively and irreversibly erode into a shrub-

Box 2-4. Quasi-Alternate States

G. Peterson

The dynamics of a system with a single stable state may approximate a system with multiple stable states if a perturbation can cause the system to persist in a slowly changing unstable state. While such a system does not have true alternative states, its dynamics and management may be similar. Semiarid grazing systems provide an example.

Competition between grasses and woody vegetation is mediated by stocking rates of cattle and sheep that graze grass but not woody vegetation. At low grazer densities, grass dominates; however, as stocking density increases, grazing may shift the competitive balance in favor of woody vegetation. If high stocking densities persist, the grass will be unable to persist and the system will be dominated by woody vegetation. This state is relatively self-maintaining, and a reduction of stocking densities does not allow grass to replace woody vegetation. However, in some conditions of relatively good soils, the woody vegetation–dominated state is not stable, because rainfall variation and the death of shrubs allow grasses to re-invade woody sites.

Woody vegetation dies back very quickly in dry years but recovers only slowly in wet years. Grass can recover much more quickly. Grass biomass can expand up to tenfold during a season by utilizing water not used by the slow-growing woody vegetation. In addition, as woody vegetation gradually dies, patches are opened that can be colonized by grasses. Over time, these patches allow fire to invade a woody patch. The grass state of this rangeland is the only stable equilibrium of such a system, but when this state is perturbed by overgrazing, the system will make a slow transition through a woody-dominated period before it returns to a grass-dominated state. High stocking levels over a time period of five to twenty years allow woody plants to replace grasses. However, during the following thirty years, the death of woody vegetation allows fire to invade, replacing woody vegetation with grasses. This type of slowly changing unstable state is not a true alternative stable state, but to a rancher who is making decisions about stocking levels, it may as well be (J. Ludwig et al. 1997; Walker 1988).

If we chose to redefine the system to include ranchers as a dynamic part of it, then the slowly changing state could, however, be converted to a true stable state. In such a case, economic reality could so lock the rancher into continued stocking of sheep that recovery would be impossible.

dominated semidesert that is sustained by low-level grazing (J. Ludwig et al. 1997; Chapter 11; Box 2-4).

Note that the α phase is the condition for the greatest uncertainty—the greatest chance of unexpected forms of renewal as well as unexpected crises. As we emphasize later, this is one of the key elements in Nature Evolving—the condition where, momentarily, novel reassortments of species in ecosystems (or recombinations of genes in cell division) generate new possibilities that are later tested. That is precisely what happens in meiosis, where novel reassortments and recombinations of genes contained within the sex cells launch novel experiments that are tested by natural selection. It is the basis of the modeling use of genetic algorithms invented by John Holland, to generate and explore novelty in economic, social, and mathematical systems (Holland 1995; Chapter 9).

r to K

In both the α and r phases, surviving residual vegetation and physical structures represent biotic legacies from the previous cycle (Franklin and MacMahon 2000). They provide a template on which the seeds from the past or from distant sources germinate. The r phase becomes rapidly dominated by a thriving biota that is adapted to high variability of microclimate and extremes of soil conditions and can further occupy unexploited territory through effective dispersal. Because of these adaptations, resilience remains high. Similarly, it is a condition in which, in the economy, the innovator sees unlimited opportunity. Or in which producers of new products can aggressively capture shares in newly opened markets. Because connectedness is low, the entities are very much influenced by external variability—both as opportunities to exploit and as constraints to bear. As a consequence, they have evolved or are selected from a pool that includes species and individuals adapted to dealing with the stresses and opportunities of a variable environment—the risk takers, the pioneers, the opportunists.

A period of contest competition among entrepreneurial pioneers and surviving species from previous cycles ensues. The ones fastest off the mark and most aggressive are the ones likely to persist. Many fail. Aggressive invasive species start to sequester ecological space. Start-up organizations, whether in businesses, research, or policy, initiate intense activity energized by a pioneer spirit and opened opportunity. Markets start to become controlled by products once they exceed about 5 percent of the potential.

This starts a progression from r to K as the winners expand, grow, and accumulate potential from resources acquired. We use the term *resources* in the broadest sense, including, for example, carbon and nutrients for the biota, production and managerial skills for the entrepreneur, marketing skills and financial capital for the producer, and physical, architectural structure for all systems. Connectedness between interrelated entities begins to increase because facilitation and contest competition between species